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CHROMOSOME NUMBERS AND POLLEN
DIAMETER VARIATION
IN *THELESPERMA* (ASTERACEAE)

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ABSTRACT

Diploid and tetraploid chromosome numbers and pollen measurements are reported for 95 collections from five taxa of *Thelesperma* (Asteraceae). These chromosome counts include the first 17 diploid (2x) reports for *T. megapotamicum* var. *ambiguum*. A correlation between ploidy level (2x, 4x) and pollen diameter (mm) is found in diploid and polyploid plants of *T. megapotamicum* and *T. simplicifolium*. In both taxa, multivalent configurations (IV, V, VI, X) are found. A recurring oversized bivalent (II) was observed in up to 23 of the 103 collections from four of the five taxa studied.

RESUMEN

En este estudio se contaron números cromosómicos diploides y tetraploides, y medidas de polen de 95 colecciones, las cuales en total agrupan cinco táxones de *Thelesperma* (Asteraceae). Los recuentos de cromosomas incluyen 17 de diploides (2x) de *T. megapotamicum* var. *ambiguum*, publicados ahora por primera vez. En plantas diploides y poliploides de *T. megapotamicum* y *T. simplicifolium* se encontró una correlación entre el nivel de ploidía (2x, 4x) y el diámetro del polen (mm). Además ambos táxones presentaron configuraciones multivalentes (IV, V, VI, X). Posiblemente en 23 de las 103 colecciones se observó una recurrencia de bivalentes (II) con tamaño incrementado, en cuatro de los cinco táxones.

Melchert (1963) included approximately 169 documented chromosome counts for 10 taxa of *Thelesperma*. Prior to the Melchert (1963) study, chromosome numbers were known for 10 of the 15 taxa recognized in his treatment, and counts of $n = 8, 9, 10, 11, 12$ and 22 were already established for *Thelesperma*. The pre-1963 counts led erroneously to the notion that every taxon of *Thelesperma* was characterized by a single chromosome number. Melchert discovered 2x dysploid series in four taxa of *Thelesperma* and dysploid diploid and polyploid plants in three taxa. The documented counts reported by Melchert (1963) were never published. About 27 chromosome counts for *Thelesperma* published in 15 papers since 1966 (see Goldblatt & Johnston

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1990, and earlier Indices to Plant Chromosome Numbers) also revealed chromosome number variation in the genus. Certain meiotic irregularities in *Thelesperma*, mostly one to five rings-of-four in diploids and polyploids, were reported by Melchert (1963), Strother (1976), Keil and Pinkava (1976), and others.

We document numerous chromosome counts from five taxa of *Thelesperma*. Most of the counts resulted from a populational study of the diploid-tetraploid *T. megapotanicum*-*T. ambiguum* complex, which was the focal point of thesis research (Greer 1997). We comment on meiotic irregularities and the correlation between ploidy level and pollen diameter in *Thelesperma*.

METHODS AND MATERIALS

Capitula for meiotic analysis were fixed in Modified Carnoy's Solution (4 chloroform: 3 ethanol: 1 glacial acetic acid; v:v:v). Standard squash techniques (Turner & Johnston 1961) and acetocarmine stain were employed in chromosomal observations. The sources of pollen for pollen size comparisons were the same as those for meiotic analyses. Pollen sizes were measured by ocular micrometer calibrated with slide micrometer such that 1 ocular unit equaled 1 μm (Greer 1997). Often up to 10–30 pollen grains were measured for a given collection.

Correlations between pollen diameter and ploidy level were established by a two-step process. A consensus measurement was estimated for the most frequent ranges of pollen diameters found in each voucher collection (inclusive and exclusive of the pollen exine, i.e., mm exinate and intinate). These consensus measurements (in mm exinate and intinate) were then plotted against the inferred ploidy levels of the respective specimens (Fig. 1).

All the voucher specimens are preserved at the Sul Ross State University Herbarium (SRSC) except for the B.L. Turner collections of *T. filifolium* var. *filifolium*, which are housed in the Herbaria of the University of Texas at Austin (TEX and LL).

RESULTS

Included are 95 original chromosome number reports for four species (five taxa) of *Thelesperma*. Specimen citations are accompanied by meiotic chromosome numbers, configurations, irregularities, and pollen diameters in Table 1. Certain capitulum characters of *T. megapotanicum* var. *megapotanicum* and *T. megapotanicum* var. *ambiguum* are included, e.g., heads radiate or discoid and disc corolla coloration, because the putative hybrids of these taxa are thought to be distinguishable by variation in these characters (Melchert 1963; Greer 1997). It is important to note that both $2x$ and $4x$ chromosome numbers and pollen grains with variable diameter were often observed

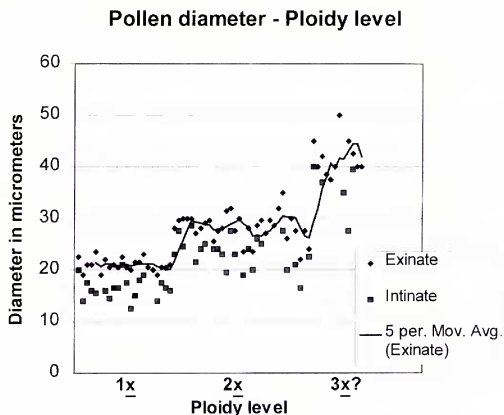


FIG. 1. Plot of exinate (small diamonds) and intinate (small squares) pollen diameter consensus measurements versus putative ploidy levels (for 60 voucher collections, Table 1): 1x pollen measurements (mean = 21 mm, s.d. = 1.23); 2x pollen measurements (mean = 28, s.d. = 2.7); 3x pollen measurements (m = 42, s.d. = 3.6). Trend line follows a five percent moving average for exinate diameters.

in the same populations and even in the same individual plants (Table 1).

The Turner collection of *T. filifolium* var. *filifolium* in Kimbel County yielded the rare euploid cytotype of $n = 11$ (Greer 1997). Most collections of *T. filifolium* var. *filifolium* have the dysploid cytotypes of $n = 9$ and $n = 8$ (Melchert 1963). This chromosome number (Greer 1997) confirms the continued existence of this rare cytotype in Kimbel County which was first reported by Melchert (1963).

DISCUSSION

The 17 diploid ($2n = 22$) chromosome counts obtained for *T. megapotamicum* var. *ambiguum* (RESULTS) represent the first diploid ($2x$) chromosome numbers reported for the taxon. Previous reports (Melchert 1963; Turner & Flyr 1966) suggested that var. *ambiguum* was exclusively tetraploid throughout its range. Melchert (1963) recognized *T. megapotamicum* and *T. ambiguum* as distinct species. He listed 42 counts for the complex, 17 diploid and tetraploid counts for *T. megapotamicum*, 19 tetraploid counts for *T. ambiguum*, and six tetraploid

TABLE 1. The meiotic chromosome numbers, configurations, irregularities, and pollen diameters with the respective taxon, source specimen collection numbers, and locations. Collections are arranged alphabetically by taxa. Observed multivalent configurations and both exinate and intinate pollen diameters are included. The putative presence of the oversized bivalent is designated by (II). Chromosome counts or pollen measurements from more than one plant are indicated as (populational). Authorities for the taxonomy are noted below¹.

Taxon & capitular characters	Locality & collection no.	Ploidy level (x=11)	Chromosome number	Pollen diameter (µm) (exinate & intinate)
<i>T. filifolium</i> var. <i>filifolium</i> Red-brown disc, radiate	Tex.: Harper County <i>Turner s.n. (a,b)</i>	2x	2n = 9H (II) 2n = 10II (II?)	
<i>T. filifolium</i> var. <i>filifolium</i> Red-brown disc, radiate	Tex.: Kimbel County <i>Turner s.n.</i>	2x	n = 11	(Anaphase I: Only one side countable)
<i>T. longipes</i> Yellow discoid	Tex.: Crockett County 5 mi N of Ozona <i>Greer 122a,b</i> (populational)	≈2x ≈4x		18–20–24 µm exinate 14–16–18 µm intinate 26–28 µm exinate 22–23 µm intinate
<i>T. megapotamicum</i> var. <i>megapotamicum</i> Yellow disc, radiate. (red-brown 75%, orange & yellow, ca. 12% each)	Tex.: Terrell County 5.5 mi E of Longfellow <i>Powell, 2671c</i> (populational)	2x	2n = 11II	
<i>T. megapotamicum</i> var. <i>megapotamicum</i> Yellow discoid	Tex.: Brewster County ~11.6 mi NE of Alpine <i>Greer 111</i>	≈2x ≈4x, 6x?		20–23(–25) µm exinate 16–18(–22–24) µm intinate 29–30(–45) µm exinate 26–29(–40) µm intinate
<i>T. megapotamicum</i> var. <i>megapotamicum</i> Yellow discoid, reddish disc lobes (red-brown at maturity)	Tex.: Brewster County ~25 mi S of Ft. Stockton <i>Powell 2735</i>	2x	2n = 11II	
<i>T. megapotamicum</i> var. <i>megapotamicum</i>	Tex.: Pecos County 3 mi E of TX 1776/11 <i>Greer 114</i>	2x ≈4x, 6x	2n = 11II (II)	18–20 µm exinate (10–)15–18 µm intinate 30 µm exinate few to 40 µm exinate
<i>T. megapotamicum</i> var. <i>megapotamicum</i> Yellow discoid	NMex.: Socorro County ~34 mi E of San Antonio <i>Powell 2528</i>	2x	2n = 11II	

¹Taxonomy with authorities: *Thelesperma* Lessing; *T. filifolium* (Hook.) A. Gray var. *filifolium*; *T. longipes* A. Gray; *T. megapotamicum* (Spreng.) O. Kuntze var. *megapotamicum*; *T. megapotamicum* (Spreng.) O. Kuntze var. *ambiguum* (A. Gray) Shinnars; *T. simplicifolium* A. Gray var. *simplicifolium*.

Taxon & capitular characters	Locality & collection no.	Ploidy level (x=11)	Chromosome number	Pollen diameter (mm) (exinate & intinate)
<i>T. megapotamicum</i> var. <i>megapotamicum</i> Yellow discoid	Tex.: Hudspeth County 12.5 mi E of Dell City <i>Powell 2831</i>	4x	2n = 22II	
<i>T. megapotamicum</i> var. <i>megapotamicum</i> Yellow discoid (~ 50% red and yellow discs)	Tex.: Presidio County 32 mi S of Marfa <i>Powell 2522</i>	4x	2n = 18II + 2IV	
<i>T. megapotamicum</i> var. <i>megapotamicum</i> Yellow discoid	Tex.: Brewster County 5 mi W of Marathon <i>Sloan and Powell 2542</i>	4x	2n = 18II + 2IV	
<i>T. megapotamicum</i> var. <i>megapotamicum</i> Yellow discoid	Tex.: Brewster County W side of Alpine <i>Greer 96</i>	4x	2n = 18II + 2IV (2II?) 2n = 22II 2n = 21II?	
<i>T. megapotamicum</i> var. <i>megapotamicum</i> Rich, golden yellow discoid.	Tex.: Brewster County W side of Alpine <i>Greer 100</i>	4x	2n = 22II 2n = 13II + 4IV? (II?)	
<i>T. megapotamicum</i> var. <i>megapotamicum</i> Yellow discoid	Tex.: Brewster County ~10 mi NE of Alpine <i>Greer 110</i>	4x	2n = 22II Anaphase I dicentric	25-30(-31) μ m exinate 18-23(-28) μ m intinate Immat.: 10 μ m exinate 6 μ m intinate
<i>T. megapotamicum</i> var. <i>megapotamicum</i> Yellow discoid	Tex.: Pecos County 2 mi E of Imperial <i>Greer 116a,b,c</i> (populational)	=4x	2n = 20-21II (?)	
<i>T. megapotamicum</i> var. <i>megapotamicum</i> Yellow discoid	Tex.: Pecos County 12.9 mi E of Imperial <i>Greer 119</i>	=4x =2x	2n = 20-21II (?)	25-35(-49 crushed) μ m exinate 20-22 μ m exinate 15-18-20 μ m intinate Dimorphic pollen in 1:1 ratio. 26-29(-31) μ m intinate
<i>T. megapotamicum</i> var. <i>megapotamicum</i> Yellow disc, radiate	Tex.: Terrell County E side of Lozier Canyon <i>Greer 169</i>	4x [=4x?] =6x?	2n = 22II 1-3 IV	23-24 μ m exinate 19-21 mm intinate 40-50 μ m exinate 25-33 μ m intinate
<i>T. megapotamicum</i> var. <i>megapotamicum</i> Yellow disc, radiate	Tex.: Terrell County W side of Lozier Canyon <i>Greer 171</i>	2x 4x	2n = 11II 2n = 22II	19-22 μ m exinate (=2x) 25-29 μ m exinate { ² 4x?}

Table 1 continued

Taxon & capitular characters	Locality & collection no.	Ploidy level (x=11)	Chromosome number	Pollen diameter (mm) (exinate & intinate)
<i>T. megapotamicum</i> var. <i>megapotamicum</i>	Tex.: Ward County 8 mi N of Jct. TX 1776/1450 <i>Greer 175</i>	2x	2n = 9II + 11V (?) (II)	
<i>T. megapotamicum</i> var. <i>megapotamicum</i>	Tex.: Ward County, TX 2 mi N of Monahans <i>Greer 177</i>	2x	2n = 11II (II) 2n = 12II? (?) 2n = 9II + 11V	
<i>T. megapotamicum</i> var. <i>megapotamicum</i> Young appearing plants (1 st year perennials?)	Tex.: Winkler County, TX 14.7 mi N of Monahans <i>Greer 179</i>	2x ≈4x	2n = 11II	Avg.: 20 μm exinate Avg.: 29–30 μm exinate
<i>T. megapotamicum</i> var. <i>megapotamicum</i>	Tex.: Winkler County 4.5 mi NE of Kermit <i>Greer 181</i>	2x	2n = 11II	
<i>T. megapotamicum</i> var. <i>megapotamicum</i>	Tex.: Winkler County 14 mi NE of Kermit <i>Greer 182</i> (populational)	2x	2n = 11II (II) 2n = 9II + 11V 2n = 5II + 3IV or 6II + 3IV (?) 2n = 4II + 2IV + 1VI 2n = 11II or 9II 11V	1 st head: Most 18–20 μm exinate (13?–)14–15 μm intinate few clusters: 27–30 μm exine 18–20 μm intinate {=4x?} 2 nd head clusters: –32 μm exinate {=4x} 3 rd + head: –35 μm exinate 25–30 μm intinate
<i>T. megapotamicum</i> var. <i>megapotamicum</i> Young plants (1 st year perennials?)	Tex.: Winkler County 16.3 mi NE of Kermit <i>Greer 183</i> (populational)	2x 4x	2n = 9II 2n = 11II (II) 2n = 9II + 11V 2n = 18II + 2IV	
<i>T. megapotamicum</i> var. <i>megapotamicum</i> Reddish involucre	Tex.: Andrews County N of Winkler-Andrews County line <i>Greer 185</i>	2x	2n = 11II (II)	
<i>T. megapotamicum</i> var. <i>megapotamicum</i>	Tex.: Andrews County 24.3 mi NE of Kermit <i>Greer 186a</i>	2x	2n = 11II 2n = 9II + 11V 2n = 10II? (II)	
<i>T. megapotamicum</i> var. <i>megapotamicum</i>	Tex.: Andrews County 24.3 mi NE of Kermit <i>Greer 186b</i>	2x	2n = 11II 2n = 10II? (II)	

Taxon & capitular characters	Locality & collection no.	Ploidy level (x=11)	Chromosome number	Pollen diameter (mm) (exinate & intinate)
<i>T. megapotamicum</i> var. <i>megapotamicum</i> Yellow discoid	Tex.: Brewster County 36.4 mi S of I-10, US 67 31 May 1995 <i>Greer 187</i>	4x	2n = 11II + 3IV + 1X 2n = 18II + 2IV 2n = 17II + 1IV + 1VI + 1VI (II?) 2n = 17II + 1IV	
<i>T. megapotamicum</i> var. <i>megapotamicum</i> Yellow discoid	Tex.: Brewster County 9.6 mi E of Marathon <i>Greer 195</i>	4x	2n = 22II (?)	
<i>T. megapotamicum</i> var. <i>megapotamicum</i> Yellow disc, radiate	Tex.: Pecos County 40.5 mi E of Marathon <i>Greer 206</i>	≈2x		(19-)21-22 μm exinate 17-18 μm intinate
<i>T. megapotamicum</i> var. <i>megapotamicum</i> Orange-yellow disc, radiate; large trilobate ray florets	Tex.: Terrell County 41.7 mi E of Marathon <i>Greer 216</i>	2x	2n = 11II	
<i>T. megapotamicum</i> var. <i>megapotamicum</i> Yellow disc, reduced radiate	Tex.: Terrell County 42.4 mi E of Marathon <i>Greer 217</i>	2x	2n = 11II	
<i>T. megapotamicum</i> var. <i>megapotamicum</i> Yellow discoid	Tex.: Terrell County >46 mi E of Marathon <i>Greer 222</i>	4x?	2n ≈ 22II (?)	
<i>T. megapotamicum</i> var. <i>megapotamicum</i> Dark yellow disc, minute ray florets	Tex.: Terrell County 51 mi E of Marathon <i>Greer 226</i>	2x	2n = 11II	
<i>T. megapotamicum</i> var. <i>megapotamicum</i> Yellow, red-tinted discoid	Tex.: Terrell County 52.4 mi E of Marathon <i>Greer 228</i>	4x	2n = 22II (?)	
<i>T. megapotamicum</i> var. <i>megapotamicum</i> Yellow disc, radiate	Tex.: Terrell County 51.5 mi E of Marathon <i>Greer 234a</i>	2x	2n = 11II	
<i>T. megapotamicum</i> var. <i>megapotamicum</i> Yellow disc, radiate	Tex.: Terrell County 51.5 mi E of Marathon <i>Greer 234b</i>	2x 4x	2n = 11II (II) 2n = 22II 2n = 20II + 1IV	
<i>T. megapotamicum</i> var. <i>megapotamicum</i> Yellow discoid	Tex.: Terrell County 29.1 mi W of Lozier Canyon <i>Greer 262</i> (populational)	4x	n = 22 Anaphase I ≥2IVs per meiocyte	25, 28-30, ~40 μm exinate {≈4x, 6x?}

Table 1 continued

Taxon & capitular characters	Locality & collection no.	Ploidy level (x=11)	Chromosome number	Pollen diameter (mm) (exinate & intinate)
<i>T. megapotaemicum</i> var. <i>megapotaemicum</i> Golden disc, very reduced radiate	Tex.: Terrell County 32.6 mi W of Lozier Canyon <i>Greer 263</i>	4x	2n = 22II lagging chromos.	
<i>T. megapotaemicum</i> var. <i>megapotaemicum</i> Reddish yellow disc, radiate (somewhat reduced), yellow style branches	Tex.: Terrell County 32.6 mi W of Lozier Canyon <i>Greer 264</i>	4x	2n = 22II (?) lagging chromos.	
<i>T. megapotaemicum</i> var. <i>megapotaemicum</i> Yellow disc, radiate (dark colored disc florets)	Tex.: Terrell County 34.0 mi W of Crozier Canyon <i>Greer 268</i>	4x	2n = 21II	
<i>T. megapotaemicum</i> var. <i>megapotaemicum</i> Yellow discoid	Tex.: Terrell County ~40+ mi W of Lozier Canyon <i>Greer 271b</i>	4x	2n = 22II (?) [=2x?, 4x, 6x?]	22-26, 40 µm exinate 20-25 µm intinate
<i>T. megapotaemicum</i> var. <i>megapotaemicum</i> Dark yellow discoid	Tex.: Val Verde County 5 mi W of Del Rio <i>Greer 155</i>	4x {6x?}	2n = 22II	25-26(-30) µm exinate (16-)18-20(-22) µm intinate (up to 35 µm intinate)
<i>T. megapotaemicum</i> var. <i>megapotaemicum</i> and var. <i>ambiguum</i> Yellow discoid; 2 orange discoid (one clump)	Tex.: Terrell County 52.4 mi E of Marathon <i>Greer 231</i> (mixed populational)	4x 2n = 12II + 5IV	2n = 17II + 2IV + 1 dicentric Anaphase I: Separated 2n = 11II + 4IV + 1VI	
<i>T. megapotaemicum</i> var. <i>ambiguum</i> Orange disc, radiate	Tex. Brewster County 5 mi W of Marathon <i>Powell 2683</i>	2x	2n = 11II	
<i>T. megapotaemicum</i> var. <i>ambiguum</i> Reddish-brown disc, radiate (mixed population of radiate & discoid)	Tex.: Brewster County near Terlingua <i>Powell 2512</i>	4x	2n = 18II + 2IV	
<i>T. megapotaemicum</i> var. <i>ambiguum</i> Red discoid	Tex.: Brewster County ~17.1 mi NE of Alpine <i>Greer 113</i>	=4x		(26-)30-33(-34) µm exinate (20-24)27-29 µm intinate variable

Taxon & capitular characters	Locality & collection no.	Ploidy level ($x=11$)	Chromosome number	Pollen diameter (mm) (exinate & intinate)
<i>T. megapotamicum</i> var. <i>ambiguum</i> Red disc, radiate; double layer ray florets	Tex.: Pecos County 40.5 mi E of Marathon <i>Greer 207</i>	2x	$2n = 11III$ (II)	
<i>T. megapotamicum</i> var. <i>ambiguum</i> Red discoid	Tex.: Terrell County 41.7 mi E of Marathon <i>Greer 213</i>	2x	$2n = 11III$	
<i>T. megapotamicum</i> var. <i>ambiguum</i> Orange disc, radiate (slender ray florets)	Tex.: Terrell County 32.6 mi W of Lozier Canyon <i>Greer 265</i>	4x	$2n = 22II$ (?)	
<i>T. megapotamicum</i> var. <i>ambiguum</i> Red-brown discoid	Tex.: Brewster County Marathon <i>Powell and Powell 2540</i>	2x	$2n = 18II + 2IV$	
<i>T. megapotamicum</i> var. <i>ambiguum</i> Red-brown discoid	Tex.: Brewster County 5 mi W of Marathon <i>Powell and Powell 2541</i>	4x	$2n = 18II + 2IV$	
<i>T. megapotamicum</i> var. <i>ambiguum</i> Orange disc, radiate; some double ray florets	Tex.: Terrell County 51.5 mi E of Marathon <i>Greer 235</i>	2x 4x	$2n = 11III$ (II?) $2n = 22II$ (2 meicytes)	
<i>T. megapotamicum</i> var. <i>ambiguum</i> Light orange disc, radiate	Tex.: Terrell County 10.2 mi W of Lozier Canyon <i>Greer 255</i>	4x	$2n = 22II$ (II) $2n = 18II + 2IV$ (II)	
<i>T. megapotamicum</i> var. <i>ambiguum</i> Orange discoid almost: 2 minute ray florets	Tex.: Terrell County 29.1 mi W of Lozier Canyon <i>Greer 259</i>	4x	$2n = 18-19II + 11V$ $2n = 22II$ (?)	
<i>T. megapotamicum</i> var. <i>ambiguum</i> Small red disc, radiate	Tex.: Terrell County 0.9 mi W of Sanderson <i>Greer 280</i>	2x	$2n = 11III$	
<i>T. megapotamicum</i> var. <i>ambiguum</i> Red disc, radiate	Tex.: Terrell County 1.1 mi W of Sanderson <i>Greer 283</i>	2x	$2n = 11III$ (2-4II)?	
<i>T. megapotamicum</i> var. <i>ambiguum</i> Reddish-brown disc, radiate	Tex.: Brewster County 70 mi S of Alpine <i>Powell and Powell 2540</i>	4x	$2n = 18II + 2IV$	
<i>T. megapotamicum</i> var. <i>ambiguum</i> Red-brown disc, radiate (red-brown 75%, orange & yellow, ca. 12% each)	Tex.: Terrell County 5.5 mi E of Longfellow <i>Powell, 2671a</i> (populational)	2x	$2n = 11III$	

Table 1 continued

Taxon & capitular characters	Locality & collection no.	Ploidy level (x=11)	Chromosome number	Pollen diameter (mm) (exinate & intinate)
<i>T. megapotamicum</i> var. <i>ambiguum</i> Orange disc, radiate (red-brown 75%, orange & yellow, ca. 12% each)	Tex.: Terrell County 5.5 mi E of Longfellow <i>Powell, 2671b</i> (populational)	2x	$2n = 11II$	
<i>T. megapotamicum</i> var. <i>ambiguum</i> Red discoid	Tex.: Brewster County 36.4 mi S of I-10, US 67 31 May 1995 <i>Greer 188a</i>	4x	$2n = 13II + 4IV$ $2n = 15II + 1IV + 1X$	
<i>T. megapotamicum</i> var. <i>ambiguum</i> Reddish-ringed discoid	Tex.: Brewster County 36.4 mi S of I-10, US 67 31 May 1995 <i>Greer 188b</i>	4x	$2n = 20II + 1IV$	
<i>T. megapotamicum</i> var. <i>ambiguum</i> Red discoid, yellow style branches	Tex.: Brewster County 12.9 mi N of Jct. US 67/90 <i>Greer 191a,b</i> (populational)	4x	$2n = 22II$ $2n \approx 20II$ lagging chromos.	
<i>T. megapotamicum</i> var. <i>ambiguum</i> Red discoid	Tex.: Brewster County 3.5 mi E of Marathon <i>Greer 192</i>	4x	$2n = 18II + 2IV$	
<i>T. megapotamicum</i> var. <i>ambiguum</i> Deep orange disc, radiate	Tex.: Terrell County 42.4 mi E of Marathon <i>Greer 218</i>	2x	$2n = 11II$	
<i>T. megapotamicum</i> var. <i>ambiguum</i> Orange discoid	Tex.: Terrell County >46 mi E of Marathon <i>Greer 220</i>	2x 4x =4x	$2n = 11II (?)$ $2n = 22II (?)$ $2n \approx 22II$	20–21 μm exinate 15–18 μm intinate 26 μm exinate (1 pollen) 20 μm intinate (1 pollen) 30 μm exinate (1 shattered pollen)
<i>T. megapotamicum</i> var. <i>ambiguum</i> Reddish discoid	Tex.: Terrell County 52.4 mi E of Marathon <i>Greer 229</i>	4x	$2n = 21II$ $2n = 22II?$	20–22, 24–26(–31) μm exinate (16–)20–22 μm intinate [$\approx 2x, 1x$]
<i>T. megapotamicum</i> var. <i>ambiguum</i> Orange disc, large ray florets	Tex.: Terrell County 52.4 mi E of Marathon <i>Greer 230</i>	2x	$2n = 11II$	

Table 1 continued

Taxon & capitular characters	Locality & collection no.	Ploidy level (x=11)	Chromosome number	Pollen diameter (mm) (exinate & intinate)
<i>T. megapotamicum</i> var. <i>ambiguum</i> Red discoid; some heads more reddish than others on the same plant	Tex.: Pecos County 33.7 mi E of Marathon <i>Greer 200a,b</i> (populational)	4x	2n = 22II (?)	
<i>T. megapotamicum</i> var. <i>ambiguum</i> Red disc, radiate	Tex.: Pecos County 38.8 mi E of Marathon <i>Greer 201</i>	2x	2n = 11II	
<i>T. megapotamicum</i> var. <i>ambiguum</i> Orange disc, radiate (large ray florets some double layered)	Tex.: Pecos County 38.8 mi E of Marathon <i>Greer 202</i>	2x	2n = 11II	
<i>T. megapotamicum</i> var. <i>ambiguum</i> Reddish-tinted discoid, orange discoid, reduced radiate	Tex.: Terrell County E side of Lozier Canyon <i>Greer 170</i> (populational)	4x =6x? =2x =2x =4x	2n = 22II	1 st Head: 26–31mm exinate 23–29 µm intinate 37–48 µm exinate 34, 42 µm intinate 2 nd Head: 17–26 µm exinate 15–21 µm intinate 3 rd Head: 23 µm exinate 19 µm intinate 28–31 µm exinate 23–27 µm intinate
<i>T. megapotamicum</i> var. <i>ambiguum</i> Reddish discoid	Tex.: Maverick County 4 mi NW of Eagle Pass <i>Greer 144a,b,c,d</i> (populational)	4x	2n = 22II (?) two Anaphase I dicentric	
<i>T. megapotamicum</i> var. <i>ambiguum</i> Radiate	Tex.: Maverick County 4.3 mi NNW of Quemado <i>Greer 145</i>	=4x	2n = 20II	
<i>T. megapotamicum</i> var. <i>ambiguum</i> Discoid	Tex.: Maverick County Rio Grande Valley, US 277 <i>Greer 146</i>	=4x =6x?		25–31mm exinate (18–19–)23–30 µm intinate 28–30 µm exine (20–)22–30 µm –36 µm (few)–39 µm
<i>T. megapotamicum</i> var. <i>ambiguum</i> Discoid, orange style branches	Tex.: Maverick County 8.1 mi NNW of Quemado <i>Greer 149</i>	=2x =4x	2n = 15II + 2IV + 1VI	19–22 µm exinate 11–18 µm intinate 20–31 µm exinate 20–22, 25, 28 µm intinate

Table 1 continued

Taxon & capitular characters	Locality & collection no.	Ploidy level (x=11)	Chromosome number	Pollen diameter (mm) (exinate & intinate)
		≈4x?		one cluster: 25–30 μm exinate 22–26 μm intinate
<i>T. megapoticum</i> var. <i>ambiguum</i> Red discoid	Tex.: Val Verde County Del Rio, US 90 <i>Greer 151</i>	≈4x {6x?}	2n = 22II? (II) At least 1 IV + II	28–29(–35) μm exinate 19–20 μm intinate
<i>T. megapoticum</i> var. <i>ambiguum</i> Orange disc, radiate	Tex.: Val Verde County 5 mi W of Del Rio <i>Greer 152</i>	≈2x	2n = 10–12II (?) Anaph. 1 dicentric lagging chromos. 2n = 22II	20–21 μm exinate (11–)15–18 μm intinate Immat.: 13–15 μm exinate
		≈4x	(one cluster)	20–25(–32) μm exinate 20–22, 26–29 μm intinate Immat.: 20–21 μm w/o exinate
<i>T. megapoticum</i> var. <i>ambiguum</i> Red discoid	Tex.: Val Verde County 5 mi W of Del Rio <i>Greer 153</i>	≈2x? 4x	2n = 11II (?) 2n = 22II 2n = 20II Anaphase 1 dicentric	21–20 μm exinate (15–)18–20 μm intinate 25–30 μm exinate 20–26 μm intinate 40 μm exinate <50 μm exinate
<i>T. megapoticum</i> var. <i>ambiguum</i> Red disc, reduced radiate	Tex.: Val Verde County 5 mi W of Del Rio <i>Greer 154</i>	≈4x		25–31(–35) μm exinate 18–24(–29) μm intinate
<i>T. megapoticum</i> var. <i>ambiguum</i> Red disc, radiate	Tex.: Val Verde County 5 mi W of Del Rio <i>Greer 157a,b,c,d,e</i> (populational)	4x	2n = 22II (?)	
<i>T. megapoticum</i> var. <i>ambiguum</i> Red-orange disc, radiate	Tex.: Val Verde County 2.0 mi W of Comstock <i>Greer 162</i>	≈4x	2n = 22II	
<i>T. megapoticum</i> var. <i>ambiguum</i> Orange discoid	Tex.: Pecos County 40.5 mi E of Marathon <i>Greer 204</i>	2x	2n = 11II 2n = 10II (?)	
<i>T. megapoticum</i> var. <i>ambiguum</i> Reddish-brown disc lobes, corolla throats yellow, radiate	Tex.: Brewster County Terlingua Creek <i>Powell 2509</i>	4x	2n = 18II + 2 IVs	

Table I continued

Taxon & capitular characters	Locality & collection no.	Ploidy level (x=11)	Chromosome number	Pollen diameter (mm) (exinate & intinate)
<i>T. megapotamicum</i> var. <i>ambiguum</i> Red-brown disc, radiate	Tex.: Brewster County 5 mi W of Marathon <i>Powell 2684</i>	2x	2n = 11II	
<i>T. simplicifolium</i> var. <i>simplicifolium</i>	Tex.: Val Verde County 25.7 mi W of Pecos River <i>Greer 166</i>	2x	2n = 10II or 11II (?)(II) (one II may two IIs overlapping)	
<i>T. simplicifolium</i> var. <i>simplicifolium</i> Yellow disc, radiate	Mexico: Coahuila, <i>Powell, D. Patterson, D. Ittner 1584</i>	4x	2n = 20II	
<i>T. simplicifolium</i> var. <i>simplicifolium</i>	Tex.: Crockett County 4.8 mi E of Jct. TX 163/190 <i>Greer 127</i>	2x ≈4x? ≈6x?	2n = 10II (II)	(22-)24-25 μm exinate 14-17 μm intinate 27 μm exinate 20-21(-23) μm intinate 42? μm exinate 37? μm intinate
<i>T. simplicifolium</i> var. <i>simplicifolium</i>	Tex.: Val Verde County 23.8 mi W of Del Rio <i>Greer 158</i>	≈2x		Avg.: 20 μm exinate (10-12)15 μm intinate
<i>T. simplicifolium</i> var. <i>simplicifolium</i>	Tex.: Kinney County 21.1 mi NW of Quemado <i>Greer 150</i>	2x =4x	2n = 10II; 2n = 10: 13?	20-22 μm exinate 15-18 μm intinate a few cells: 25, 31 μm exinate, -23 μm
<i>T. simplicifolium</i> var. <i>simplicifolium</i> Yellow disc, radiate Curvicarpum achene form	Tex.: Menard County 1 mi E of TX 29/83 <i>Greer 137</i>	2x	2n = 10II Anaphase I lagging chromosomes of one bivalent (II)	
<i>T. simplicifolium</i> var. <i>simplicifolium</i> Yellow disc, radiate Curvicarpum achene form	Tex.: Menard County 1 mi E of TX 29/83 <i>Greer 138</i>	≈2x ≈6x?		18-20 μm exinate 35-36(-40) μm exinate base of echinations: 30 μm
<i>T. simplicifolium</i> var. <i>simplicifolium</i>	Tex.: Maverick County Rio Grande Valley, US 277 <i>Greer 147</i>	2x {≈4x?}	2n = 11II (II)	20-23(-29, 30) μm exinate 15-17 μm intinate
<i>T. simplicifolium</i> var. <i>simplicifolium</i> Yellow disc, large overlapping ray florets	Tex.: Terrell County 0.2 mi W of Lozier Canyon <i>Greer 243</i>	2x 4x	2n ≈ 11II 2n = 20II	20-21-24 μm exinate (13-)16-20 μm intinate

Table 1 continued

Taxon & capitular characters	Locality & collection no.	Ploidy level ($x=11$)	Chromosome number	Pollen diameter (mm) (exinate & intinate)
<i>T. simplicifolium</i>	Tex.: Val Verde	2x	$2n = 20(?)$	21–22 μm exinate
var. <i>simplicifolium</i>	County 0.7 mi W of Pecos River Greer 163	$\approx 4x$	$2n = 10II (3II?)$	14–16 μm intinate 26–28(–29–30) μm exinate 22–24(–26) μm intinate

counts for putative hybrids between the taxa. Because of their remarkable morphological similarity, identical meiotic cytologies ($2n = 22, 44$ with multivalents), and the ease with which they apparently interbreed where sympatric, *T. megapotamicum* and *T. ambiguum* are best treated as varieties (Greer 1997). The only reliable distinguishing characteristics are range, the slightly reduced habit of var. *ambiguum*, and disc coloration. Disc florets of var. *megapotamicum* are yellow and heads generally are discoid; disc florets of var. *ambiguum* are red-brown and heads are generally yellow-radiate.

The reports (Table 1) for the *T. megapotamicum* complex provide an expanded understanding of how diploid and polyploid distribution in the species is structured, especially in Texas. *Thelesperma megapotamicum* var. *megapotamicum* is almost exclusively diploid ($2n = 22$) with yellow, discoid heads in most of its range, which extends from Nebraska, Colorado, and Wyoming west to Arizona, south across Trans-Pecos Texas into central Mexico, and east to northwest Texas (Melchert 1963). In the predominant portion of its range which extends from south Texas and near the Rio Grande Valley west into Val Verde County, *T. megapotamicum* var. *ambiguum* is largely tetraploid ($2n = 44$) with red-brown disc corollas and large, yellow ray florets. However, west of the Pecos River, mixed diploid and tetraploid populations of var. *ambiguum* occur from western Val Verde County through Terrell and Brewster counties (Greer 1997). The floral morphology of these populations of var. *ambiguum* vary from radiate with red-brown discs, discoid orange, radiate orange, to discoid red-brown. Along this same axis, var. *megapotamicum* plants are also often diploid ($2n = 22$) with yellow discs and ray corollas. Populations of var. *megapotamicum* elsewhere in the Trans-Pecos are mostly tetraploid ($2n = 44$) with yellow discoid heads, although there are occasional plants with yellow discs and yellow ray florets, often reduced in length.

Melchert (1963) interpreted plants from this area resembling both var. *megapotamicum* and var. *ambiguum* as hybrids or intergrades between the taxa. He found only tetraploids in this area. This region of apparently extensive morphological intergradation seems to mark the sympatric overlap of the

ranges of var. *megapotamicum* and var. *ambiguum* from western Val Verde County west into Brewster County. The intergradation is so smooth and continuous that morphotypes were difficult to assign taxonomically.

Origins of polyploidy. The origins of polyploidy in *T. megapotamicum* remain uncertain. Variation in floral character combinations in the sympatric region, high fertility, and the absence of univalents or trivalents in meiotic observations, suggest that allopolyploidy is more likely than autopolyploidy in var. *ambiguum* (Greer 1997). Because of the lack of morphological differentiation between diploids and tetraploids, however, polyploidy in the typical yellow discoid var. *megapotamicum* seems more likely to be autopolyploid. For similar reasons, autopolyploidy also seems more likely in other polyploid taxa of *Thelesperma* such as *T. simplicifolium* and *T. longipes* (Greer 1997).

Multivalent configurations have been observed at meiosis in diploid (Keil & Pinkava 1976; Greer 1997; Results) and in tetraploid (Melchert 1963; Strother 1976; Powell & Powell 1977; Greer 1997; Results) cytotypes of both *T. megapotamicum* var. *megapotamicum* and *T. megapotamicum* var. *ambiguum*. Melchert (1963) reported that in tetraploids, two rings-of-four (IV) were most common, and that one and three rings-of-four also were observed. In this study, we report that widely variable numbers of apparent ring and chain quadrivalents (IV), hexavalents (VI), and even decavalents (X) were found in populations of var. *megapotamicum* and var. *ambiguum* (Greer 1997). Anaphase segregation was essentially balanced and fertility remained high in spite of the multivalents (Melchert 1963) and the occasional occurrence of dicentric chromosomes (Table 1; Greer 1997).

Large bivalent. A persistent large bivalent (II) was observed in meiotic preparations in up to 23 of the 103 collections (Table 1; Greer 1997), most noticeably in preparations from diploid plants. Such an oversized bivalent has been observed in *T. megapotamicum* var. *megapotamicum*, *T. megapotamicum* var. *ambiguum*, *T. simplicifolium* var. *simplicifolium*, and *T. filifolium* var. *filifolium* (Greer 1997). An oversized bivalent is also plainly visible in Melchert's (1963) meiotic camera lucida figures of the above taxa as well as in *T. longipes*, *T. filifolium* var. *intermedium*, and possibly also in *T. burridgeanum* (Greer 1997). Melchert (1963) did not call attention to the large bivalent. In one collection of *T. simplicifolium* var. *simplicifolium* (Greer 137; Table 1), the chromosomes of an oversized bivalent lagged in anaphase I. The lagging and dicentric chromosomes observed (Table 1) may be associated with the large bivalent. A large bivalent would be more frequently expected to lag and to undergo paracentric inversions because of its length. The large bivalent may be a result of a massively unequal reciprocal translocation that occurred early in the evolution of *Thelesperma* (Greer 1997).

Pollen diameter variation. Pollen diameter size variations seem to reflect

the ploidy levels of the plants that produced them (Greer 1997). From diploid plants ($2x$) of *T. megapotamicum*, the broad range of pollen diameters for presumed $1x$ pollen ($1x$ gametophytes) was 17–26 μm exinate and 11–21 μm intinate. From tetraploid plants, the range of pollen diameters for presumed $2x$ pollen ($2x$ gametophytes) was approximately 20–35 μm exinate and 18–29 μm intinate. Rare pollen found in preparations with even larger diameters, 30–50 μm exinate and 25–42 μm intinate, have been attributed tentatively to $3x$ pollen ($3x$ gametophytes). (See Fig. 1).

Diploid plants of *T. megapotamicum* occasionally were found to produce unreduced $2x$ pollen (ca. 24–30 μm exinate) along with the more abundant $1x$ pollen (18–24 μm exinate). In Andrews and Winkler counties where var. *megapotamicum* is known to occur only as a diploid, discrete clusters of larger pollen were seen in meiotic preparations, suggesting that localized tetraploid ($4x$) microsporangial tissues are producing clusters of unreduced $2x$ gametophytes. Plants of both var. *megapotamicum* and var. *ambiguum* from Brewster, Terrell, and Val Verde counties, where populations are typically tetraploid, consistently produce pollen of both sizes (ca. 24–30 μm ; ca. 18–22 μm) in a nearly 1:1 ratio of putative $1x$ and $2x$ pollen. In tetraploids of *T. megapotamicum* larger than normal pollen (30–35 μm) were occasionally observed, suggesting that tetraploids also may be producing unreduced gametophytes ($3x?$, Fig. 1).

The same kind of ploidy level—pollen diameter variation was also observed in *T. simplicifolium* var. *simplicifolium*, which has both diploid and tetraploid cytotypes. The correlation between known chromosome numbers and pollen sizes suggests that in certain species of *Thelesperma* a given ploidy level may predominate in a specific population or plant, while gametophytes of different ploidy levels are being also produced (Greer 1997). Similar production of unreduced gametes has been reported by Beaman (1957) in *Townsendia* (Asteraceae) and Powell and Sikes (1975) in *Perityle* (Asteraceae).

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